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Variability in successive backcross generations of oats

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VARIABILITY IN SUCCESSIVE BACKCROSS GENERATIONS OF OATS

by

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Dean of Graduate College

Iowa State University
Of Science and Technology
Ames, Iowa

1959

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INTRODUCTION

Backcrossing is a breeding system whereby the hybrid is crossed to one of the parental genotypes for one or more progeny generations. In general, this technique has two unique uses: (a) to add one or several simply inherited characters to an otherwise satisfactory strain, and (b) in testcrosses to determine genetic ratios, linkage and crossover percentages.

In a practical backcrossing program certain offspring which possess the desired characters are selected for further crossing to the recurrent parent. On the other hand, the theory of backcrossing is based upon unselected populations of infinite size.

It was the purpose of this study to determine whether the means and variances of an unselected[a] sample of lines from several backcross generations would conform to those postulated by theory.

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[a]Unselected is used here to mean that no selection was knowingly practiced.

REVIEW OF LITERATURE

Backcrossing dates back to the time of the discovery of the particulate nature of inheritance by Mendel (18). Griffin as cited by Ware (36, p.667) used backcrossing in cotton breeding as early as 1867. Jennings (13) gave the quantitative results of the backcrossing system as follows:

If the original parents are AA and aa and the progeny are always mated back to one parent, the frequency of the recurrent parent genotype is $\frac{2^n - 1}{2^n}$, of the non-recurrent genotype is 0, and of the heterozygote is $\frac{1}{2^n}$ where n = number of backcross generations. Briggs (2), and Riddle and Baker (25) later expanded the formula of Jennings (13) to include the number of factor pairs as follows:

$$\% \text{ homozygosity} = \left(\frac{2^m - 1}{2^m}\right)^n$$

where: m = number of backcross generations and

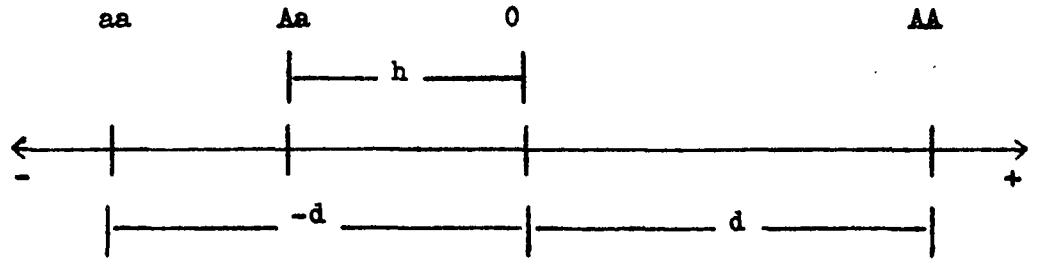
n = number of heterozygous factor pairs.

Wright (37) using the method of path coefficients arrived at an identical solution.

It remained, however, for Harlan and Pope (9) to point out the place of backcrossing in cereal breeding with experiments involving the smooth awn character in barley. This work stimulated the thought of many plant breeders. Richey (23) published the theory of convergent improvement, which is essentially reciprocal backcrossing, in corn. Later, Richey and Sprague (24), Murphy (19), and Hayes et al. (12) reported that convergent improvement was successful in improving inbred lines of corn.

Mather (17, pp. 68-71) published the biometrical expectations of

reciprocal backcrosses. Using the following model:



He states "the contributions of gene A - a to the mean of the two backcrosses, as measured from the midparent, will be $B_1 = 1/2(d_a + h_a)$ and $B_2 = 1/2(h_a - d_a)$, where B_1 is the backcross to the AA parent which gives the plus deviation, and B_2 that to the aa parent. The contributions of A - a to the variances of the backcrosses are $B_1 = 1/4(d_a - h_a)^2$ and $B_2 = 1/4(d_a + h_a)^2$. The contributions of d and h to these variances cannot be separated as they stand, but if the variances are summed, A - a contributes $1/2(d_a^2 + h_a^2)$ to the total, and the contributions of d and h can then be separated."

The primary advantage of backcrossing over selfing is that a higher percentage of homozygotes result (2). In the F_2 of a single cross, either parent is expected once in 4^n plants, whereas in the Bc_1, the recurrent parent is expected once in 2^n number of plants. To quote Knight (15, p. 77) "the essential value of backcrossing is that it provides a mean of limiting the heterogeneity which would result from 'straight' crosses between two types, making it possible to produce a hybrid similar to whichever of the two varieties has the more valuable genetic constitution, yet containing desirable characters transferred from the other parent. Backcrossing obviates the necessity for rigid selection generation after generation in F_2, F_3, F_4, etc., by progressively and

automatically rendering the hybrid more and more homogeneous."

Briggs (1) reported success in transferring bunt resistance from the Martin to Baart variety of wheat. He (3) reported excellent progress in producing better wheat varieties with the backcross system, and proposed the use of backcrosses to form isogenic lines to determine the effect of different genes on yield.

Briggs and Allard (4) state three basic requirements for a backcross breeding program: (a) a satisfactory recurrent parent, (b) retention of the intensity of the character under transfer through several backcrosses, and (c) the genotype of the recurrent parent must be reconstituted in a reasonable number of backcrosses with small populations. The expression of a gene may vary with different genetic backgrounds according to Simpson and Weindling (28) and Smith (29) and apparently there is no way of predicting the gene expression on a given background without trying it.

Others who have successfully used the backcross system on agricultural crops are Emsweller and Jones (6), Johnson and Hayes (14), Suneson et al. (31), Suneson (30) and Valleau (34,35). Thomas (33) has given a comprehensive review of backcrossing in tobacco, tomato, cotton and potatoes.

Backcrossing appears to have little use in transferring quantitative characters unless they are controlled by only one or two major genes. However, the California workers were successful in transferring genes for maturity and height from Romona to Baart wheat, and Powers (21,22) was able to transfer quantitative characters in tomatoes. Everson (7) and Suneson et al. (32) reported a major yield gene in barley which could

be transferred by backcrossing since it was linked to genes for rachilla hair length and awn barbing.

Mather (16) calculated for several probability levels the number of backcross progeny necessary to assure the breeder that the gene being transferred will be present in the population. The use of these tables was illustrated by Harrington (10) and Hayes et al. (11).

The usefulness of the backcross technique in studying linkage relationships of genes and chromosome mapping has been demonstrated by Burnham and Cartledge (5). According to Briggs and Allard (4, p. 134) the backcross method is more effective than selfing in breaking linkages between desirable and undesirable genes. They state "in any well executed backcross program, undesirable linkages may be expected to be broken in a portion of the derived lines, even if the crossover value is as small as 1 percent and the undesirable allele is not expressed."

MATERIALS AND METHODS

The recurrent and non-recurrent oat varieties used in this study were Cherokee and P.I. 185785, respectively. Cherokee (C.I. 5444) was selected from the cross D69 x Bond. It is early maturing, short in height, susceptible to race 202 of crown rust, and produces plump, white grain of good test weight. P.I. 185785 (C.I. 6952) was introduced into North America from Uruguay. It is late maturing, tall in height, resistant to race 202 of crown rust and produces long, slender, red grain of low test weight.

Cherokee and P.I. 185785 are both allo hexaploid varieties with 21 pairs of chromosomes (20,27). Further, both parents are self pollinated and are considered to be homogeneous lines.

The F_1 between Cherokee and P.I. 185785 was made in 1953 resulting in 13 hybrid seeds. Plants from these F_1 seeds were backcrossed to Cherokee to give the Bc_1[a] generation which in turn was backcrossed to Cherokee, etc., until 4 backcross generations were available. In addition to backcrossing to each plant, F_2 seed was also saved and stored so that all crosses could be grown in a common yield test. The number of lines in each backcross generation is shown in table 1.

Pedigrees were kept so that each oat strain could be traced to the proper Bc_1, Bc_2, Bc_3 or Bc_4 family. This was necessary so that the

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[a] Bc_1 = P.I. 185785 x Cherokee^2 = first backcross
Bc_2 = P.I. 185785 x Cherokee^3 = second backcross
Bc_3 = P.I. 185785 x Cherokee^4 = third backcross
Bc_4 = P.I. 185785 x Cherokee^5 = fourth backcross.

Table 1. Number of progenies tested in each backcross generation.

Backcross no.	No. of progenies
1st	25
2nd	110
3rd	215
4th	275

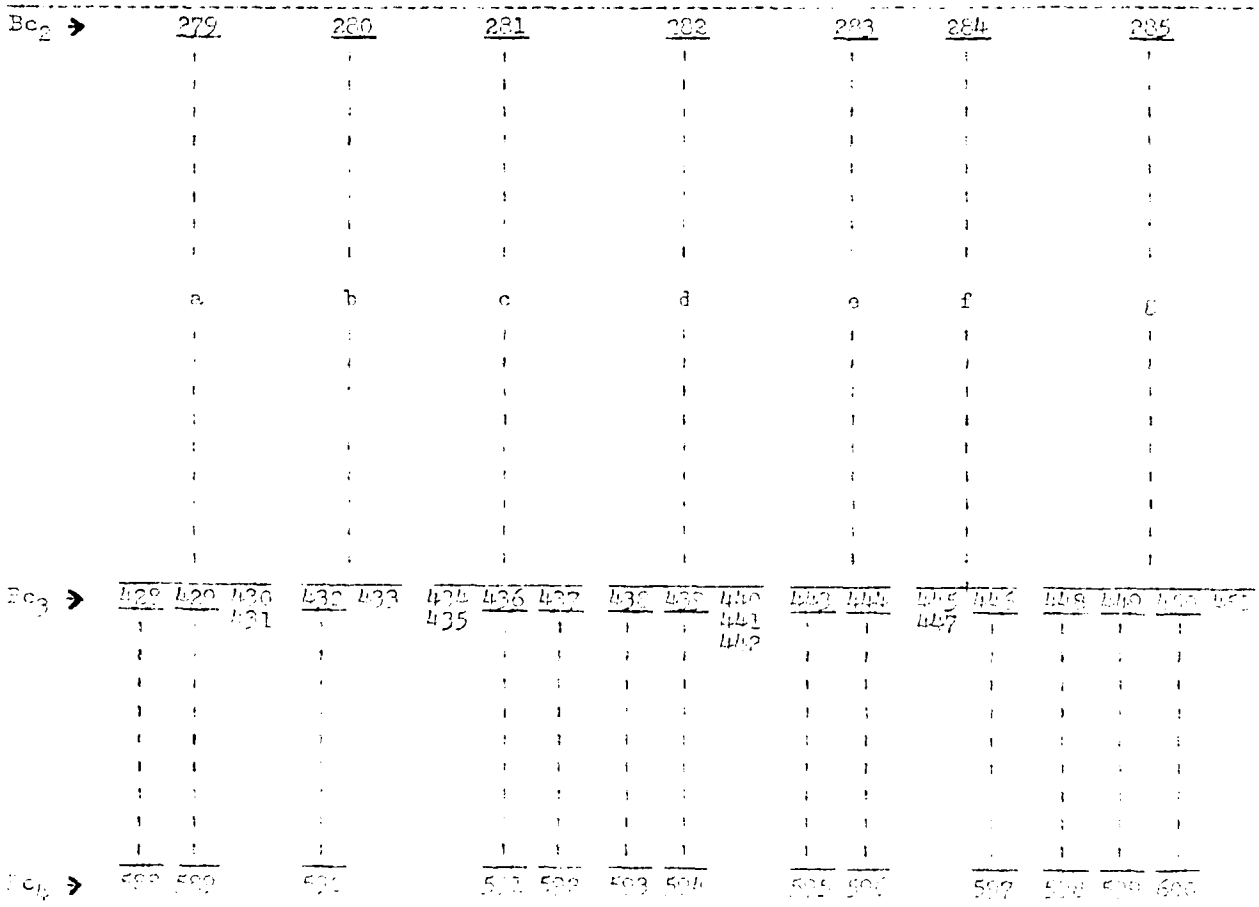
variances could be assigned to the proper within and between family categories. The pedigrees of all lines are shown in figure 1.

The crossing was completed in 1956 and the seed for the 4 backcross generations grown for increase at Aberdeen, Idaho in 1957. An experiment including 625 backcross lines (in the F_2 or F_3 generation), P.I. 185785 entered 10 times, and Cherokee 17 times, making a total of 652 entries, was grown in 1958. The experimental design was a randomized block with 8 replications, 4 grown at Ames and 4 at Kanawha, Iowa. The plot size was one hill with a 1-foot spacing between hills (26). Thirty seeds were sown in each plot which was equivalent to a planting rate of 3 bushels per acre.

Each replication was 30 x 22 feet including 8 dummy plots to bring the number to 660 per replication. At each location, the experiment was surrounded by 3 rows of hills to serve as competition and border.

Growing conditions for oats were good to excellent at Ames and Kanahwa in 1958. The rainfall distribution was variable with a short supply early in the growing season and an abundant supply in the later

Figure 1. The complete hierarchy of all families through four successive backcross generations.


Be2 →
279
280
281
282
283
284
285
a
b
c
d
e
f
Be3 →
429 430 431
432 433
434 435 436 437
438 439 440 441 442
443 444
445 447 446
448 449 450 451
Be4 →
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601
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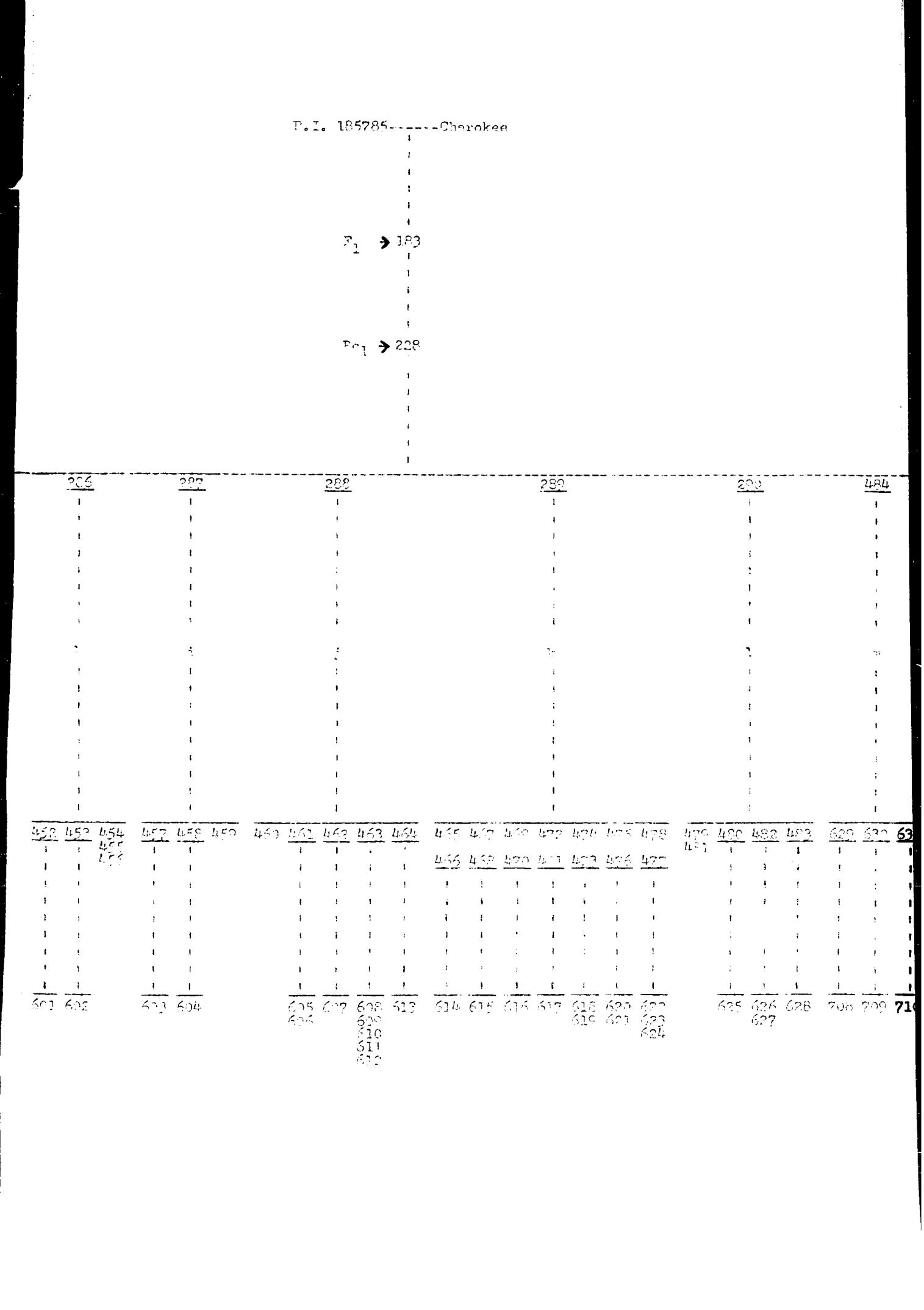
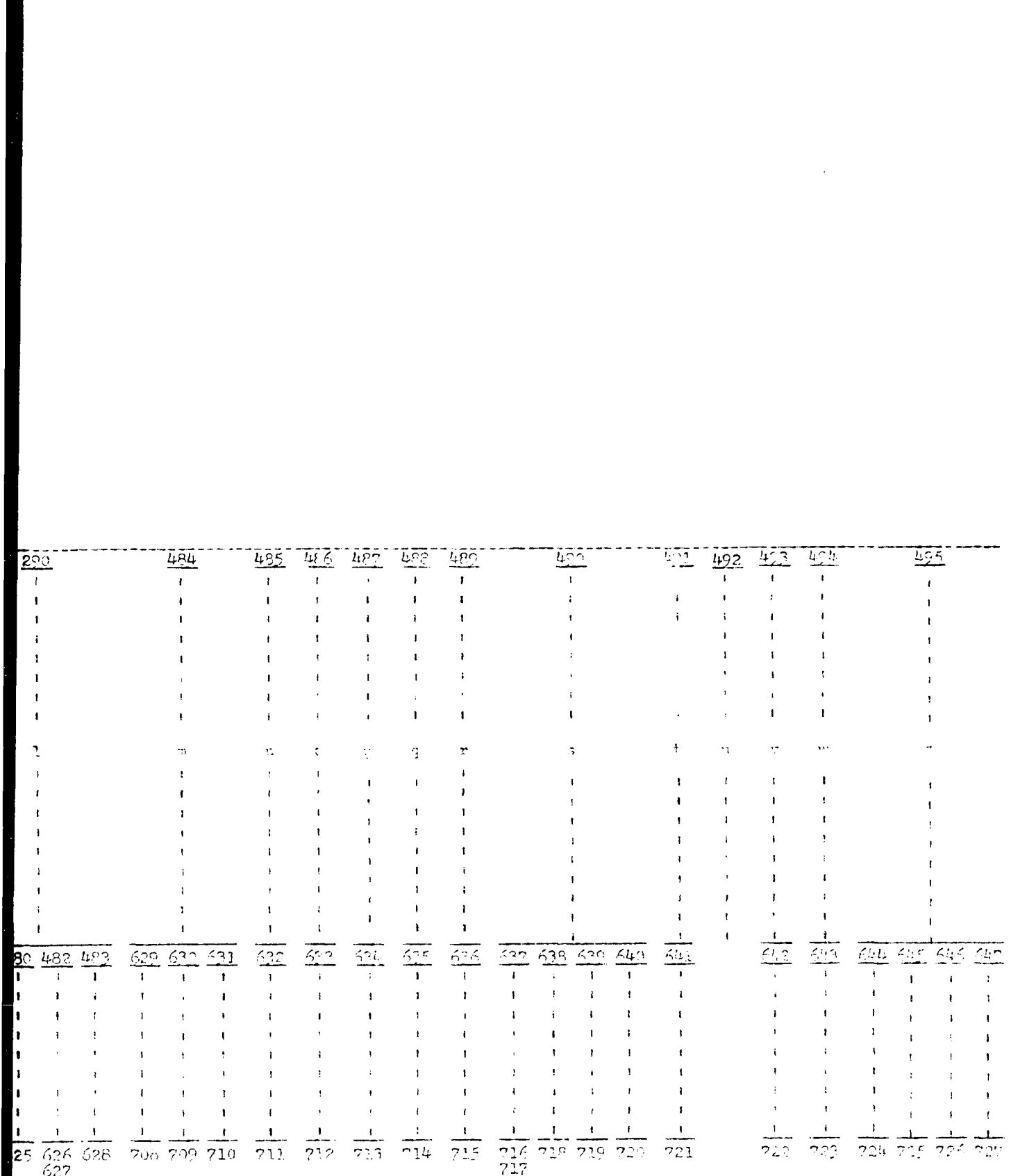
603 604
605 606
607
608 609 610


P.I. 185785------Cherokee
F_1 → 183
F_{C_1} → 228
206
222
288
289
290
484
452 453 454 455 456
457 458 459
460 461 462 463 464
465 466 467 468 469 470 471 472 473 474 475 476 477 478 479
480 481 482 483
629 630 631
501 502
503 504
505 506 507 508 509 510 511 512 513
514 515 516 517 518 519 520 521 522 523 524
525 526 527 528
706 709 710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part. The plots at Ames received one sprinkler irrigation early in the season. Since the experiment included lines both resistant and susceptible to crown rust and other foliar diseases, it was sprayed with a fungicide (Zineb) so that disease reaction would not confound the expression of the characters measured.

The measurements taken were date of heading and plant height on the 4 replications grown at Ames, and grain yield on all 8 replications. Weight-per-volume was measured as 2 replications since it was necessary to combine the seed of an entry from four replications to order to have enough to take a weight-per-volume measurement. These measurements were taken in a glass cylinder measuring 7.7 mm in diameter and 3.9 in depth. Date of heading was recorded when 50 percent of the heads in a plot were completely emerged from the boot; plant height was measured in inches from ground level to the panicle tips; and grain yield was recorded in grams per plot. Each of these characters is multigenically inherited and subject to continuous distribution, both characteristic of quantitative characters.

RESULTS AND DISCUSSION

Means and Variances

The mean squares from the analysis of variance of the data for grain yield, date of heading, plant height and weight per volume are presented in table 2.

All of the mean squares involving lines within generations, except for the parental entries, were highly significant. While the general trend was for the mean squares to be reduced with a greater number of backcrosses, the reduction was not pronounced until the Bc_4. The mean squares for height and weight-per-volume were quite constant in the Bc_1, Bc_2 and Bc_3 generations but reduced in the Bc_4. For some unknown reason, yield and date of heading mean squares were low in the Bc_2 and Bc_4 but high in the Bc_3 generation. One or two Bc_1 families caused most of this abnormality.

The mean squares for the two parents approximated the error variance. P.I. 185785 showed significant variation for date of heading but this may have been due to its poor adaptation to Iowa growing conditions.

One of the important factors in a backcrossing program is the rapidity with which the performance of the hybrid lines return to the level of the recurrent parent. This can be studied in two ways: (a) by the means and variances of the different generations and (b) by the range of performance among lines within backcross generations.

The mean squares for Cherokee vs. the means of the backcross generations are presented in table 3. Since the Cherokee parent contributes one-half of the germplasm to each backcross, the mean squares measuring

Table 2. Mean squares for four quantitative characters among lines within generations.

Source of variation	Degrees of freedom	Characters			
		Yield	Date	Height	Wt./vol.
Entries	649	165**	99**	13**	21**
Entries x loc.	649	37	--	--	--
Between generations	5	2133**	7558**	468**	486**
Among entries in generation	644	150**	41**	10**	18**
Among Bc_1 entries	24	277**	138**	12**	26**
Among Bc_2 entries	108	127**	33**	12**	22**
Among Bc_3 entries	213	198**	80**	11**	22**
Among Bc_4 entries	274	121**	9**	8**	12**
Among Cherokee entries	16	27	0	2	2
Among P.I. 185785 entries	9	28	3*	1	--
Error	---[a]	26	1.4	2	5

[a]D.f. for error are as follows: Yield = 3894; Date = 1953; Height = 1953; and Wt./vol. = 637.

For this and all following tables:

*Exceeds the 5% level of probability

**Exceeds the 1% level of probability

differences between Cherokee and the backcross means should decrease with successive generations of backcrossing. All mean squares were significant, and date of heading, height and weight-per-volume mean squares decreased as expected, especially in the Bc_4. However, the trend for yield was for the mean squares to increase.

The mean performance for the parental strains (table 4) differed widely for each of the characters measured. In the backcross material, the means for date of heading, height and weight-per-volume progressed toward the Cherokee parent gradually (figure 2, table 4), but perhaps not as rapidly as expected since by Bc_4 the germplasm contribution from

Table 3. Mean squares for Cherokee vs. the backcross generation means for four quantitative characters.[a]

Source of variation	Degrees of freedom	Characters			
		Yield	Date	Height	Wt./vol.
Between generations	5	2133**	7558**	468**	486**
Cherokee vs. Bc_1	1	518**	554**	350**	539**
Cherokee vs. Bc_2	1	1102**	95**	466**	697**
Cherokee vs. Bc_3	1	1015**	67**	297**	592**
Cherokee vs. Bc_4	1	1357**	28**	259**	182**
Cherokee vs. P.I. 185785	1	3100**	25,301**	1840**	---

[a]Non orthogonal breakdown of sum of squares.

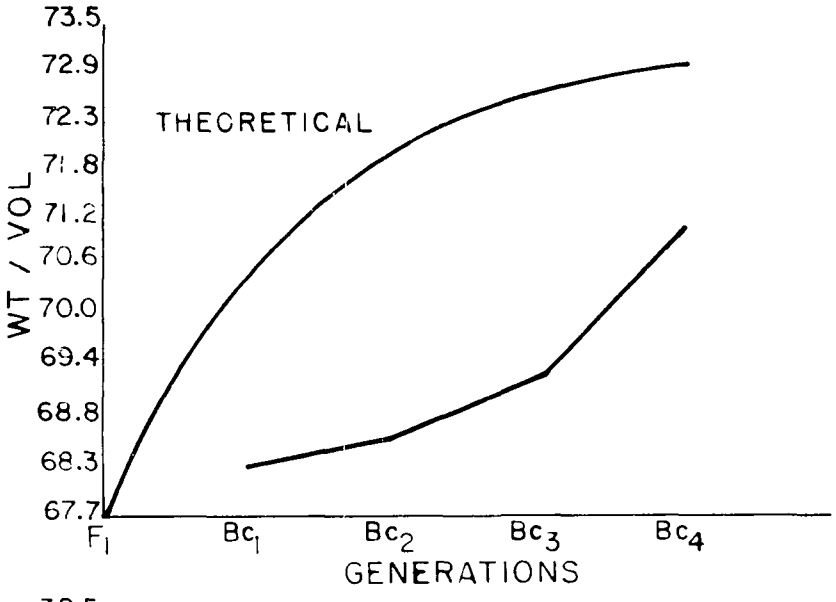
Table 4. Means of four quantitative characters for the parents and four backcross generations.

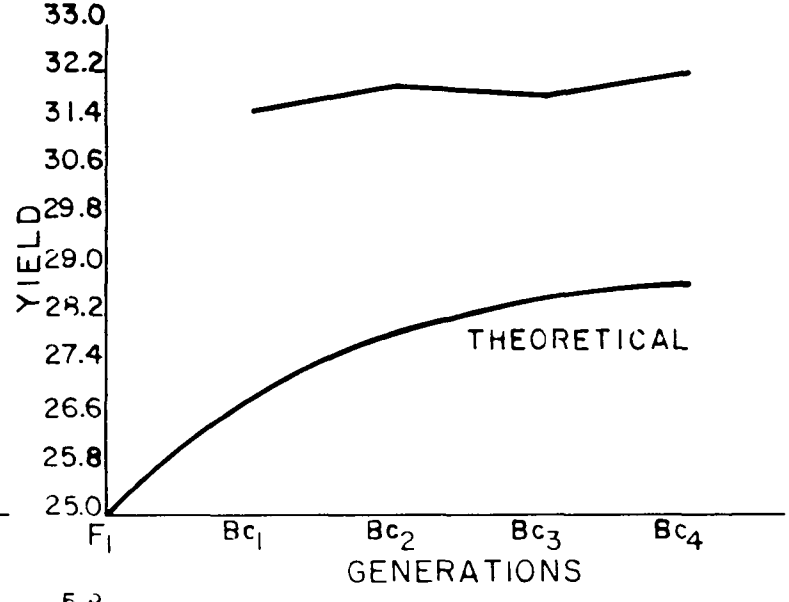
Parents and backcross generations	No. of entries	Means			
		Yield	Date	Height	Wt./vol.
Entries	652	32	7.3	35	70
Bc_1	25	32	8.8	36	68
Bc_2	110	32	7.0	36	69
Bc_3	215	32	6.8	35	69
Bc_4	275	32	6.5	35	71
Cherokee	17	29	5.8	33	74
P.I. 185785	10	21	37.5	41	62*[a]

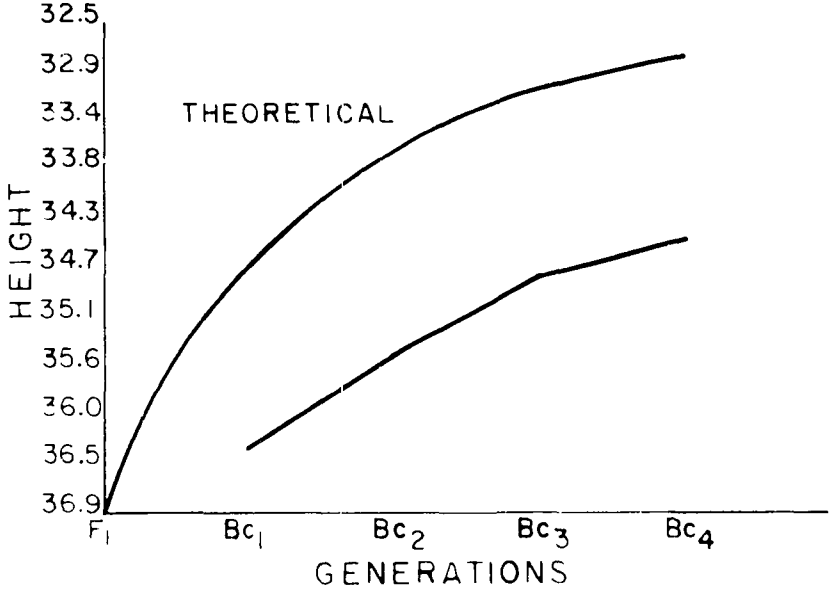
[a]This is an estimate over all eight replications due to a short supply of seed.

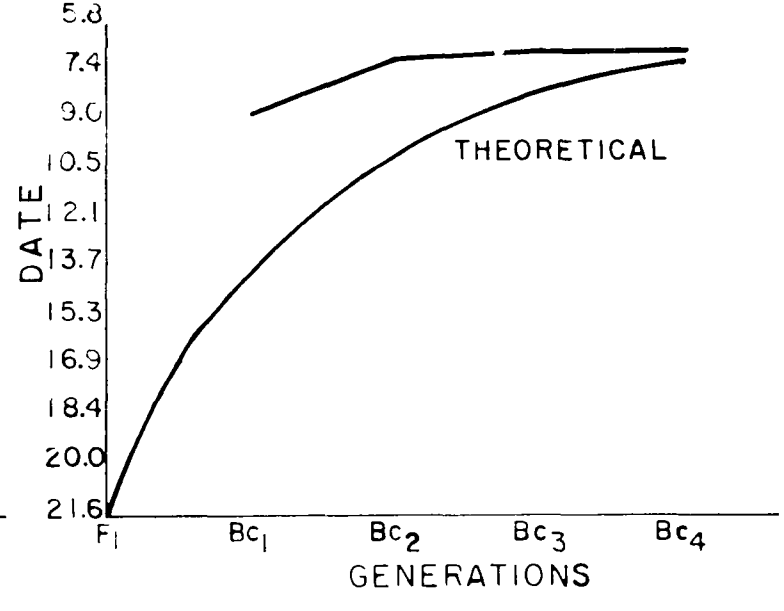
Cherokee to the backcross plants should be nearly 97 percent. The theoretical 3 percent contributed by the P.I. 185785 parent was apparently very potent in expression or it is possible that some unknown selection pressure was operating which may have caused retention of a larger percentage of the P.I. 185785 germplasm than was expected.

Figure 2. Actual and theoretical means for four quantitative characters in the backcross generations.


73.5
72.9
72.3
71.8
71.2
70.6
70.0
69.4
68.8
68.3
67.7
WT / VOL
THEORETICAL
F1
Bc1
Bc2
Bc3
Bc4
GENERATIONS


33.0
32.2
31.4
30.6
29.8
29.0
28.2
27.4
26.6
25.8
25.0
YIELD
THEORETICAL
F1
Bc1
Bc2
Bc3
Bc4
GENERATIONS


32.5
32.9
33.4
33.8
34.3
34.7
35.1
35.6
36.0
36.5
36.9
HEIGHT
THEORETICAL
F1
Bc1
Bc2
Bc3
Bc4
GENERATIONS

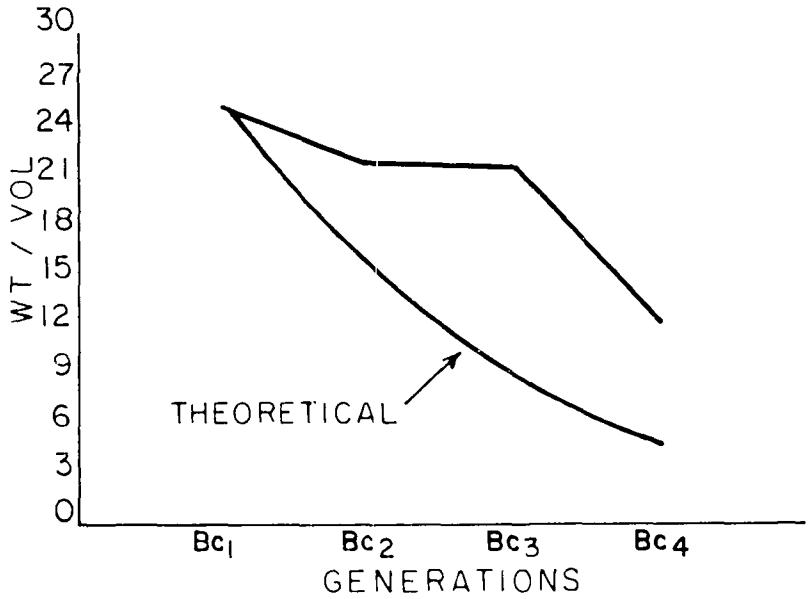

5.8
7.4
9.0
10.5
12.1
13.7
15.3
16.9
18.4
20.0
21.6
DATE
THEORETICAL
F1
Bc1
Bc2
Bc3
Bc4
GENERATIONS

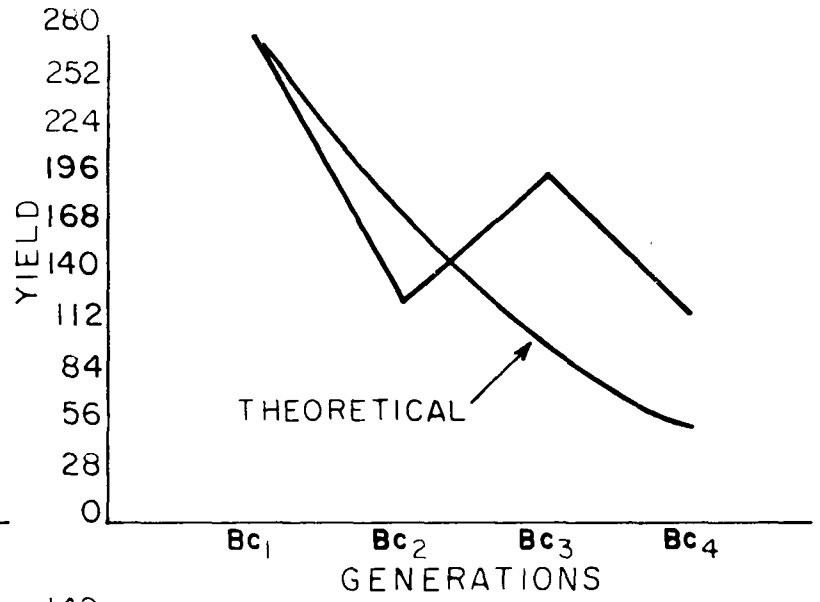
Also included in figure 2 are the expected means for the four quantitative characters in each backcross generation. The theoretical curve was constructed on the assumption of additive gene action with the midparent value representing the F_1 and the Cherokee value as the performance after an infinite number of generations of backcrossing. The expected progress toward the Cherokee value was one-half of the remainder for each succeeding generation. The trend in mean values for the weight-per-volume suggest dominance for low weight-per-volume contributed by the P.I. 185785 parent. In contrast, the actual curve of means for heading date suggest dominance of earliness from the Cherokee parent.

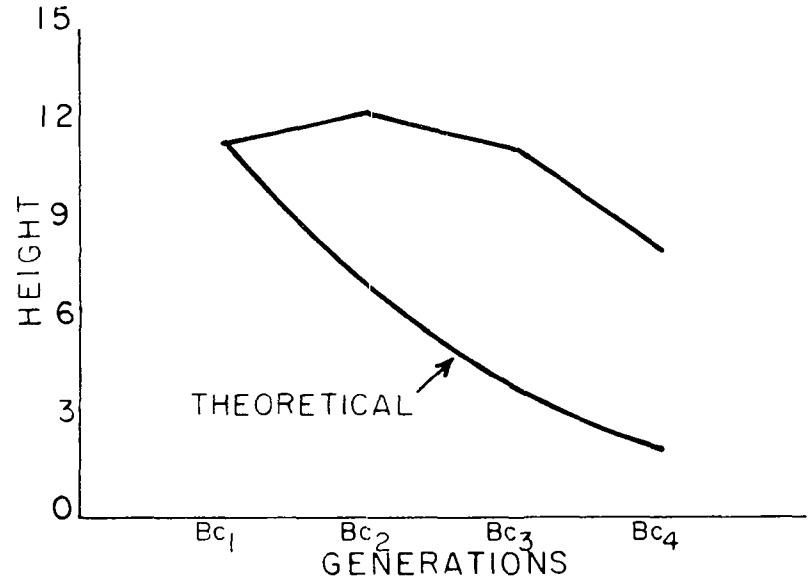
The mean yield per plot was approximately 32 grams for all four backcross generations. This value was significantly above both parental strains. Such a heterotic effect might be expected in the early backcross generations since yield is subject to geometric epistasis (8). However, the yield nevertheless should have regressed toward the recurrent parent mean to a certain extent with four backcrosses. Since yield is probably affected by a large number of genes, the proportion of individuals which would be reconstituted like Cherokee would be small even in the Bc_4. This suggests that there would be ample opportunity for considerable geometric epistasis as late as the Bc_4 and, therefore, the yield level of the backcross generations would not regress very rapidly. The curve of height means is somewhat parallel to the theoretical curve but at a lower level.

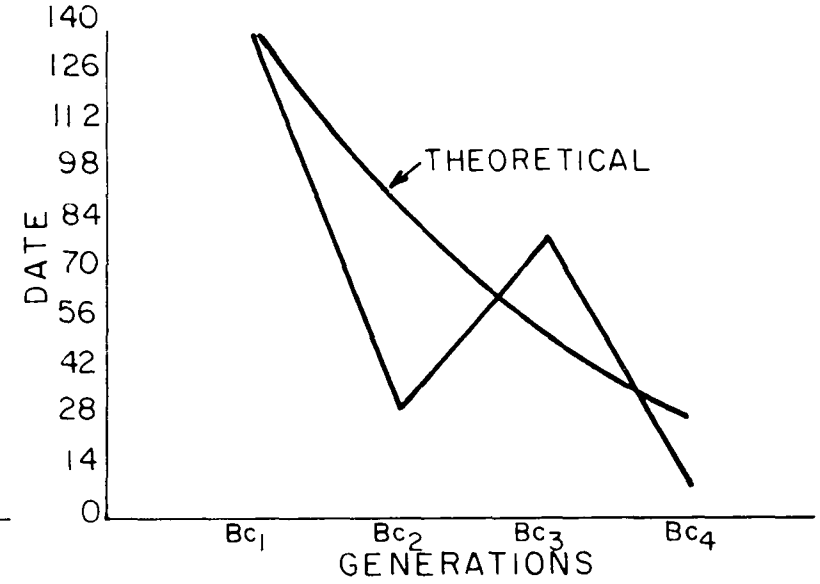
The theoretical and actual total variances for the four characters in each generation are plotted in figure 3. The theoretical curves for

Figure 3. Actual and theoretical variances for four quantitative characters in four backcross generations.


30
27
24
21
18
15
12
9
6
3
0
WT / VOL
THEORETICAL
Bc1
Bc2
Bc3
Bc4
GENERATIONS


280
252
224
196
168
140
112
84
56
28
0
YIELD
THEORETICAL
Bc1
Bc2
Bc3
Bc4
GENERATIONS


15
12
9
6
3
0
HEIGHT
THEORETICAL
Bc1
Bc2
Bc3
Bc4
GENERATIONS


140
126
112
98
84
70
56
42
28
14
0
DATE
THEORETICAL
Bc1
Bc2
Bc3
Bc4
GENERATIONS

yield and date of heading were constructed on the basis of epistatic effects, whereas those for height and weight-per-volume were based on dominance or additive gene action (the reason to be discussed in conjunction with tables 10 and 11). For construction of the theoretical curves, the true variance was assumed to be the same as that of the Bc_1. Needless to say, this assumption may be subject to considerable error, but it should not affect comparisons where trends of actual and theoretical curves are involved.

The theoretical curves for epistasis were calculated on two and three gene models with varying gene effects. The expected reduction of total variance for succeeding backcross generations was less than one-half and the variance reductions from one generation to the next were less with epistasis than with dominance or additive gene action. In all four characters the total variances were reduced with continued backcrossing.

For height and weight-per-volume, the actual variances were not reduced as rapidly as expected. The variances for yield and date of heading were sporadic. As noted earlier, the Bc_3 variances were larger than those in Bc_2. The only reasonable explanation for the large Bc_3 variance is that a divergent sample of gametes was obtained when the backcross was made on the Bc_2.

Tables 5, 6 and 7 contain the mean squares within individual Bc_1 families for the Bc_2, Bc_3 and Bc_4 generations. While most Bc_4 families are less variable than their Bc_3 progenitors, several Bc_3 families were more variable than their Bc_2 ancestors.

Part of the explanation for variances higher than expected in Bc_3

Table 5. Mean squares for four quantitative characters within Bc_1 families in the Bc_2 generation.

Source of variation	Degrees of freedom	Characters			
		Yield	Date	Height	Wt./vol.
Bc_2 generation	109	127**	33**	12**	22**
Within family a	3	157**	240**	12**	20**
Within family b	--	--	--	--	--
Within family c	1	30	3	12**	36**
Within family d	4	87	6**	7**	9
Within family e	1	12	0	6	0
Within family f	1	663**	1	12**	0
Within family g	9	235**	33**	13**	26**
Within family h	4	13	3	2	4
Within family i	1	53	2	2	1
Within family j	4	75*	1	6*	21**
Within family k	12	125**	23**	13**	16**
Within family l	3	123**	12**	14**	7
Within family m	2	31	26**	21**	29**
Within family n	3	46	1	0	29**
Within family o	2	92**	18**	1	4
Within family p	4	12	1	2	25**
Within family q	3	76*	2	7*	13
Within family r	3	28	25**	9**	46**
Within family s	3	13	4*	1	14*
Within family t	1	1	10**	18**	6
Within family u	4	174**	14**	16**	15*
Within family v	7	30	1	2	12*
Within family w	8	53*	2	5**	13*
Within family z	4	150**	3	3	9
Between Bc_2 families	22	238**	89**	30**	41**

families may be due to the fact that P.I. 185785 was not adapted to Iowa growing conditions, and the measurements taken directly on this variety did not express its true potential of performance. When a portion of the P.I. 185785 germplasm was substituted onto an essentially Cherokee background, it had an opportunity for a maximum expression. Another contributing factor may be a divergent "gametic sample" in the Bc_2.

Table 6. Mean squares for four quantitative characters within Bc_1 families in the Bc_3 generation.

Source of variation	Degrees of freedom	Characters			
		Yield	Date	Height	Wt./vol.
Bc_3 generation	214	198**	80**	11**	22**
Within family a	6	125**	167**	33**	42**
Within family b	6	31	9**	9**	5
Within family c	13	118**	14**	2	16**
Within family d	19	164**	6**	4**	26**
Within family e	2	683**	3	9*	43**
Within family f	5	290**	108**	15**	23**
Within family g	8	1121**	1018**	31**	36**
Within family h	15	236**	13**	5**	15**
Within family i	7	113**	3	3	8
Within family j	9	105**	2	7**	18**
Within family k	30	86**	25**	12**	13**
Within family l	10	336**	44**	28**	23**
Within family m	14	146**	2	6**	13**
Within family n	1	81	3	3	2
Within family o	5	22	1	2	1
Within family p	3	43	2	1	2
Within family q	6	67*	3*	6**	5
Within family r	1	0	2	0	30**
Within family s	16	48*	1	2	9*
Within family t	2	2	1	1	11
Within family u	--	—	—	—	—
Within family v	5	73*	3	2	2
Within family w	1	1	0	1	25**
Within family z	8	76**	2	2	6
Between Bc_3 families	22	422**	252**	33**	78**

To illustrate, the major source of Bc_2 variation in family a (table 8 and figure 4) was due to entry 027 whose mean heading date was from two to four times larger than the other Bc_2 entries. (The numbers enclosed parenthetically are entry numbers and the adjacent numbers are the dates of heading.) This shows the gametic variability available from the Bc_1. Entry 027 gave one gamete which produced a late zygote

Table 7. Mean squares for four quantitative characters within Bc_1 families in the Bc_4 generation.

Source of variation	Degrees of freedom	Characters			
		Yield	Date	Height	Wt./vol.
Bc_4 generation	274	121**	9**	8**	12**
Within family a	12	95**	20**	15**	4
Within family b	6	55*	5**	4*	4
Within family c	11	45	1	3	6
Within family d	3	47	4*	1	2
Within family e	5	313**	1	3	1
Within family f	2	2	1	2	2
Within family g	11	103**	25**	24**	33**
Within family h	7	108**	6**	2	8
Within family i	8	74**	3	4*	4
Within family j	63	91**	2	4**	7
Within family k	55	28	2	7**	5
Within family l	17	120**	7**	11**	5
Within family m	9	157**	1	4*	14**
Within family n	1	14	6*	3	9
Within family o	2	53	2	6*	4
Within family p	0	0	0	0	0
Within family q	1	6	0	0	2
Within family r	5	47	0	5*	6
Within family s	13	199**	4**	5*	12**
Within family t	5	62*	0	3	5
Within family u	--	--	--	--	--
Within family v	2	50	3	1	1
Within family w	1	1	0	6*	1
Within family z	13	32	2	3*	11*
Between Bc_4 families	22	570**	638**	33**	62**

and one which was early, so the gametic range was still highly variable for date of heading genes in the Bc_2. Although the Bc_2 should have contained seven-eighths Cherokee genotype, segregation produced gametes which were quite unlike Cherokee. However, it is evident that the sample of gametes obtained in the Bc_3 generation contained an abnormally high number of "non-Cherokee" gametes. In the Bc_3, the proportion of the "rare" gametes should have become small enough so that the sample

Table 8. Mean squares for date of heading for lines within family a.

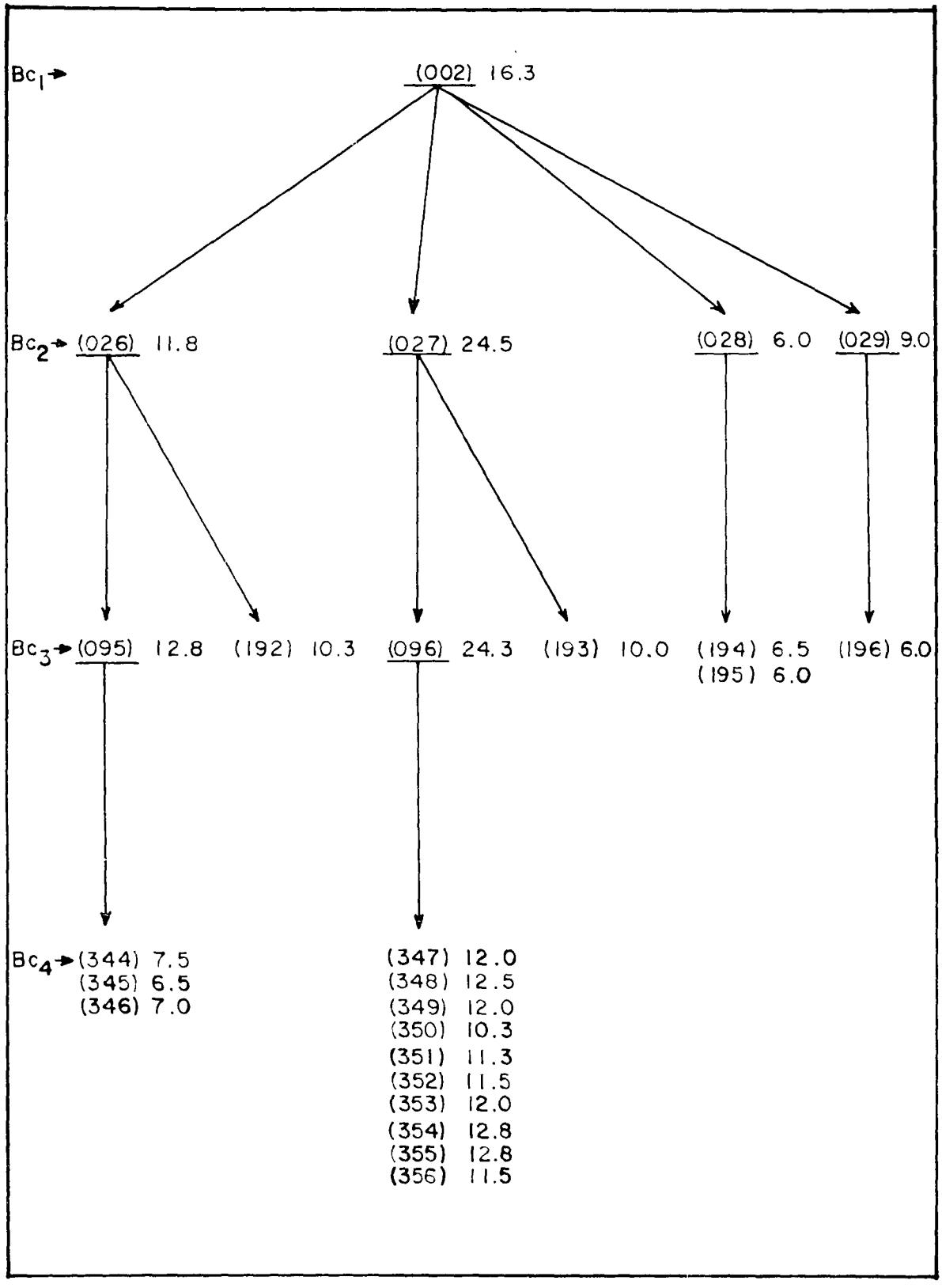
Source of variation	Degrees of freedom	Characters			
		Yield	Date	Height	Wt./vol.
		Bc_2			
Family a	3	157**	240**	12**	20**
		Bc_3			
Family a	6	125**	167**	33**	42**
Within Bc_3 family 1	1	5	13**	3	4
Within Bc_3 family 2	1	324**	406**	41**	21**
Within Bc_3 family 3	1	68	0	2	1
Between Bc_3 families	3	118**	194**	50**	76**
		Bc_4			
Family a	12	95**	20**	15**	4
Within Bc_4 family 1	2	30	1	3	2
Within Bc_4 family 2	9	73**	2	7**	3
Between Bc_4 families	1	425**	217**	118**	17

included in this study would not be expected to include them very often; and they were only occasionally found in the Bc_4 progeny. This was more true for date of heading and yield than for the other two characters.

Since backcross theory is based only upon the assumption of additive genetic effects, it is further possible that genetic systems such as dominance, epistasis, linkage, etc. could have produced the observed variability within families of the second and third backcross generations. However, just what effect such genetic systems would have on backcross populations has not been established.

The mean squares between Bc_1 families in the Bc_2, Bc_3 and Bc_4 for

Figure 4. Entry numbers (in parentheses) and means for dates of heading for progenies in family a.


Bc1
(002) 16.3
Bc2
(026) 11.8
(027) 24.5
(028) 6.0
(029) 9.0
Bc3
(095) 12.8
(192) 10.3
(096) 24.3
(193) 10.0
(194) 6.5
(195) 6.0
(196) 6.0
Bc4
(344) 7.5
(345) 6.5
(346) 7.0
(347) 12.0
(348) 12.5
(349) 12.0
(350) 10.3
(351) 11.3
(352) 11.5
(353) 12.0
(354) 12.8
(355) 12.8
(356) 11.5

the four quantitative characters are given in table 9. The variation between families did not change significantly from one generation to the next for height and weight-per-volume, but it did increase significantly for the other two characters, date of heading and grain yield. The magnitude of increase of the variances between Bc_1 families was rapid for these latter two characters. The F test showed that the Bc_4 variance for yield was significantly greater than the Bc_2 variance. For date of heading, the variance between families was significantly greater in each successive backcross.

The trend expected for between family variances over generations was determined using a two gene model based upon different types of gene action (table 10). The non-recurrent parent was represented by aaBB and the recurrent parent by AAbb, and the genes were given the following effects: $A = 3$; $B = 5$; $a = b = 1$. The variances between Bc_1 families should have remained constant over all backcross generations with either dominance or additive genetic effects. Since the variances between Bc_1 families for height and weight-per-volume did not differ significantly, the genes affecting these two characters probably displayed dominance and/or interacted additively. The variances between Bc_1 families for yield and date of heading increased with successive backcross generations indicating epistatic gene action. For yield, this was expected since it was subject to geometric epistasis, but previous studies on date of heading have given no indication of epistasis.

Transgressive segregation is frequently observed for quantitative character in the progeny of crosses in cereals, but generally not when the parents are as diverse as those used in this study. Such observations

Table 9. Mean squares between Bc_1 families for quantitative characters in the Bc_2, Bc_3 and Bc_4.

Source of variation	Degrees of freedom	Characters			
		Yield	Date	Height	Wt./vol.
Between Bc_2 families	22	238**	89**	30**	41**
Between Bc_3 families	22	422**	252**	33**	78**
Between Bc_4 families	22	570**	638**	33**	62**

Table 10. Theoretical variances between Bc_1 families in four backcross generations with epistasis, dominance or additive gene action, using a two gene model and selfing to form F_2.

Generation	Variances between Bc1 families[a]		
	Epistasis	Dominance	Additive
Bc_1	23.40	3.08	6.67
Bc_2	24.25	3.08	6.67
Bc_3	25.56	3.08	6.67
Bc_4	26.26	3.08	6.67

[a]The effect of the genes are as follows: A = 3; B = 5; a = b = 1.

are expected even less in backcross progeny. Be this as it may, transgressive segregation was observed as late as the Bc_3. Date of heading data illustrates this phenomena, although it is exhibited by the other characters also.

In the Bc_3 generation of family g (figure 5), some entries transgressed the parental range for date of heading. Table 11 contains the

Figure 5. Entry numbers (in parentheses) and dates of heading for progenies in family g.

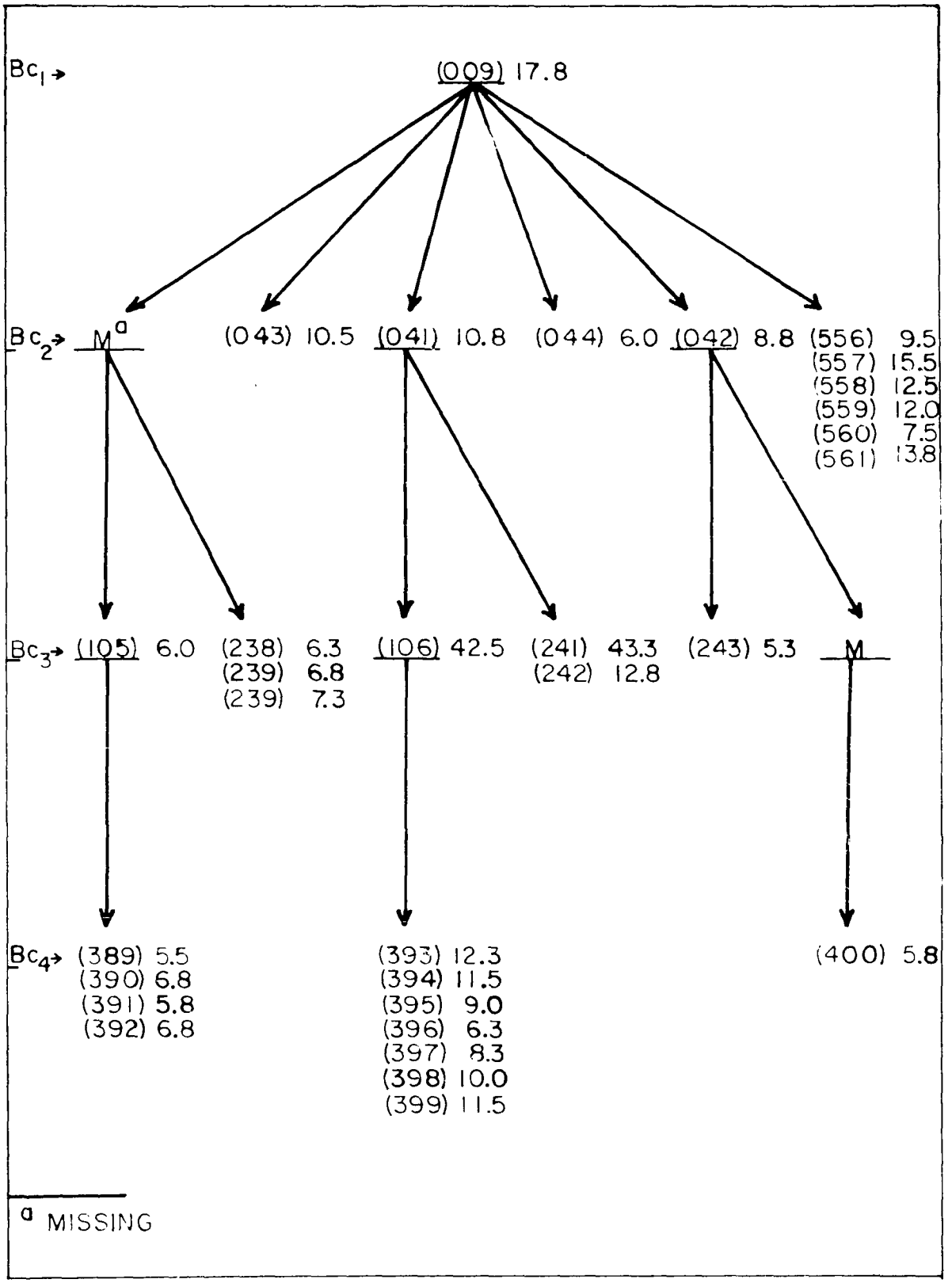

Bc1 →
(009) 17.8
Bc2→
M[a]
(043) 10.5
(041) 10.8
(044) 6.0
(042) 8.8
(556) 9.5
(557) 15.5
(558) 12.5
(559) 12.0
(560) 7.5
(561) 13.8
Bc3→
(105) 6.0
(238) 6.3
(239) 6.8
(239) 7.3
(106) 42.5
(241) 43.3
(242) 12.8
(243) 5.3
M
Bc4→
(389) 5.5
(390) 6.8
(391) 5.8
(392) 6.8
(393) 12.3
(394) 11.5
(395) 9.0
(396) 6.3
(397) 8.3
(398) 10.0
(399) 11.5
(400) 5.8
[a] MISSING

Table 11. Mean squares for date of heading for lines within family g.

Source of variation	Degrees of freedom	Characters			
		Yield	Date	Height	Wt./vol.
		Bc_2			
Family g	9	235**	33**	13**	26**
		Bc_3			
Family g	8	1121**	1018**	31**	36**
Within Bc_3 family 1	3	38	1	1	20*
Within Bc_3 family 2	2	1393**	1211**	7*	--
Between Bc_3 families	3	2023**	1905**	115**	52**
		Bc_4			
Family g	11	103**	25**	15**	33**
Within Bc_4 family 1	3	25	2	2	11
Within Bc_4 family 2	6	6	18**	24**	5
Between Bc_4 families	2	512**	81**	8*	150**

mean square analysis for these data. The heading date of entry 241 was 43.3 compared to 37.5 for P.I. 185785. In contrast, entry 243 was earlier than Cherokee (5.8). The extremely late lines were unexpected since the gametes which contributed to the late zygotes in the Bc_3 were produced from a fairly early Bc_2 plant. Aberrant gametic sampling seems to be the only possible explanation for this phenomenon. The Bc_3 entries 106, 241 and 242 with heading dates of 42.5, 43.3 and 12.8, respectively, were progenies from the cross Cherokee x Bc_2 entry 041 for which the heading dates were 5.8 and 10.3, respectively. While errors of pedigree and classification are possible in any experiment, this does not appear to be the case here since entries 106 and 241 both trace to the same parents.

Selection

From a practical standpoint, the rapidity with which the mean values for various characters in the backcross material returned to the Cherokee parental values was of limited importance. Even though the Bc_4 mean values for yield, height and weight-per-volume were considerably divergent from Cherokee, some lines should have been nearly identical to the recurrent parent. Selection for the recurrent parent type would be easier with additional backcrosses.

In the field, it would be possible to select plants for continued backcrossing which were more like the recurrent parent than the average of the hybrid population. For example, plants could have been selected which were most like Cherokee for date of heading and height before it was necessary to cross. Yield and weight-per-volume could be determined only when the plants were ripe; so, selection for these two characters would result in the loss of a year's time in crossing. Therefore, it would be most expedient to select for the first two characters only.

Five families were selected in the first backcross which were nearly the same as Cherokee for height and heading date. These families were compared with Cherokee through the four backcross generations (table 12). Selection for Bc_1 lines which were like Cherokee for heading date and height was effective in retaining these two characters near the Cherokee phenotype in the three subsequent backcross generations. The mean yield of the selected lines was closer to Cherokee than in the unselected families; but the reverse was true for weight-per-volume. The mean squares for "Cherokee vs. selected families" were considerably

Table 12. Mean squares from analysis of Cherokee vs. selected families and Cherokee vs. unselected families in the Bc_2, Bc_3 and Bc_4.

Source of variation	Degrees of freedom	Characters			
		Yield	Date	Height	Wt./vol.
		Bc_2			
Between selected families	3	171*	14	1	30
Cherokee vs. selected families	1	41	1	96	309**
Cherokee vs. unselected families	1	1556**	117**	514**	703**
Among lines in selected families	12	58	10	10	18
Among lines in unselected families	75	106	21	8	18
		Bc_3			
Between selected families	3	306	7	14	73
Cherokee vs. selected families	1	258	1	134**	1037**
Cherokee vs. unselected families	1	1129**	85	311**	465**
Among lines in selected families	25	186	3	6	12
Among lines in unselected families	167	170	69	9	18
		Bc_4			
Between selected families	3	365	4	1	21
Cherokee vs. selected families	1	41	2	56**	355**
Cherokee vs. unselected families	1	1558**	31**	277**	156**
Among lines in selected families	20	220	3	1	11
Among lines in unselected families	232	70	5	7	7

smaller than those for "Cherokee vs. unselected families" in both of the selected characters and yield. The most likely explanation for the selection of Cherokee type backcross lines for heading date and height being effective in obtaining types which are also like Cherokee in yield would be linkage drag. Genes which were responsible for the "Cherokee heading date and height" were linked with genes for yield and therefore, selection for the first two characters "dragged" along many Cherokee yield genes.

When oat plants were grown in the greenhouse, height was not very heritable, so this character could not be used to select Cherokee type plants with good precision. However, date of heading is heritable in the greenhouse and could be used as an effective selection criterion. Since most of the oat crossing is done in the greenhouse, the above idea was pursued in a selection experiment. Three Bc_1 families were selected, one early, one like Cherokee, and one late for date of heading. The means and ranges for these families in each generation are presented in table 13. In many cases, the family range for a character was smaller than the recurrent parent range, especially in the Bc_4. In general, selection for either early (family c) or late (family f) heading date was detrimental to mean yield although family c exceeded the recurrent parent in yield in the Bc_4. Height regressed toward the recurrent parent quite rapidly.

Selection for the recurrent parent heading date in family f after the Bc_1 would have missed the entry in the Bc_2 which yielded 43 grams per plot. This entry produced progeny yielding up to 39 grams in the Bc_3 but was not used to produce Bc_4 progeny. Selection for the recurrent

Table 13. Mean and range for four quantitative characters in each backcross generation for three families with selection for heading date in each backcross.

Backcross generation	Mean				Range			
	Yield	Date	Height	Wt./vol.	Yield	Date	Height	Wt./vol.
				Family c				
Bc_1	28	2.0	35	72	---	----	---	---
Bc_2	28	4.2	34	68	26-29	3.5-4.8	33-36	65-71
Bc_3	27	5.9	34	68	25-29	5.3-6.5	33-34	67-68
Bc_4	33	5.9	34	69	31-38	5.5-6.8	33-35	68-71
				Family f				
Bc_1	23	23.8	39	65	---	----	---	---
Bc_2	36	11.8	38	65	30-43	11.3-12.0	37-40	65-66
Bc_3	24	6.5	35	67	---	----	---	---
Bc_4	20	7.3	34	68	19-20	7.0-7.5	34-35	67-69
				Family s				
Bc_1	37	5.3	36	72	---	----	---	---
Bc_2	33	5.5	34	71	31-34	4.5-6.8	34-35	68-74
Bc_3	33	6.1	34	73	31-34	5.5-6.8	34-35	71-75
Bc_4	31	6.3	33	73	30-32	5.8-6.8	33	72-73
				Cherokee				
	29	5.8	33	74	26-33	5.5-6.3	32-34	72-75

parent heading date in family s caused all attributes to regress the recurrent parent phenotype.

In general, it appears that selection for date of heading and height, if possible, would result in recapturing the recurrent parent characteristics more rapidly than if random selection of plants for backcrossing were practiced.

Another way to measure whether selection might be effective would be through the correlations between generations. The correlation coefficients of family means for all combinations of the four backcross generations for yield, height, date of heading and weight-per-volume are given in table 14. For date of heading, the correlations were significant and very high for all comparisons. This further indicates that selection for date of heading in one backcross generation would be effective in returning the backcross progenies to the Cherokee type more rapidly than if crosses were made at random. All of the height correlations were significant, but not as high as those for date of heading. However, selection for height in any or all of the backcross generations should make the regression toward the recurrent parent more rapid.

The correlations between Bc_2, Bc_3, and Bc_4 for weight-per-volume were highly significant indicating a good relationship between these generations for this character. However, the Bc_1 was significantly correlated with only the Bc_2. Although several of the correlation coefficients for yield were significant the relationship between generations for this character were, in general, not very good.

Although with a sufficient number of backcross generations the plant breeder is assured of recovering the recurrent parent phenotype,

Table 14. Correlation coefficients among four backcross generations for four characters.

	Bc_2	Bc_3	Bc_4	Bc_2	Bc_3	Bc_4
		Yield			Date	
Bc_1	.30	.57**	.45*	.87**	.87**	.69**
Bc_2		.23	.13		.82**	.87**
Bc_3			.55**			.72**
		Height			Wt./vol.	
Bc_1	.76**	.52*	.57**	.65**	.37	.40
Bc_2		.73**	.62**		.59**	.75**
Bc_3			.48*			.61**

any procedure which would reduce the recovery time would be desirable. Selection of backcross lines in each generation which are most like the recurrent parent may reduce the number of backcrosses necessary to attain the desired goal. This study indicated that phenotypic expression of one backcross generation is well correlated with the next generation for date of heading and height. Furthermore, selection for the "Cherokee type" expression of these characters also resulted in the yield of the selected lines being closer to the Cherokee performance than was the case in the backcross population as a whole.

Linkage Study

Backcrossing has been used frequently in oats to transfer rust resistance into adapted varieties. In backcrossing to add rust resistance, selection for resistant progenies is essential in order to keep

the population size manageable while retaining progeny that carry a worthwhile intensity of resistance. If desirable or undesirable genes from the non-recurrent parent were closely linked to the resistance gene, selection for rust resistance would be either beneficial or harmful, respectively, to the primary objective. A beneficial example was found by Suneson et al. (32) where high yield genes were closely linked with the semi-smooth awn (rr) gene in barley.

Since the non-recurrent parent used in this study was so poorly adapted in Iowa, it seemed likely that only undesirable genes would be linked to the crown rust resistance gene being transferred to Cherokee. If such were the case, and if linkage were important, the mean performance for the four characters measured would not be as close to Cherokee in the resistant as in the susceptible backcross lines.

In the Bc_1, 8 entries were resistant to crown rust race 202 and 15 were susceptible. In the Bc_2 and Bc_3 (table 15), the resistant and susceptible lines were not significantly different for any of the four agronomic characters measured. In the Bc_4, the means of the resistant and susceptible groups were significantly different for date of heading, height, and weight-per-volume. This significance could be important since the means of the resistant lines were nearer to Cherokee than were the susceptible line means. However, the differences were very small, 0.6 of an inch in height, 0.3 of a day in heading date, 0.5 of a gram in weight-per-volume, and probably of little consequence. Apparently, detrimental or beneficial genes from the non-recurrent parent which might be linked to the gene for crown rust resistance were either non-existant or affected the four characters measured very little.

Table 15. Mean squares from analysis of resistant vs. susceptible families in the Bc_2, Bc_3 and Bc_4.

Source of variation	Degrees of freedom	Characters			
		Yield	Date	Height	Wt./vol.
		Bc_2			
Total	109	127*	33**	12*	22
Resistant vs. susceptible	1	30	33	3	79
Between resistant families	7	176	74**	25**	38*
Between susceptible families	14	285*	101**	35**	46**
Among lines in families	87	98	19	8	17
		Bc_3			
Total	214	198	80*	11*	22*
Resistant vs. susceptible	1	239	6	3	30
Between resistant families	7	344	251**	51**	94**
Between susceptible families	14	477**	241**	27**	72**
Among lines in families	192	172	62	9	16
		Bc_4			
Total	274	121**	9**	8*	12**
Resistant vs. susceptible	1	48	205**	85**	322**
Between resistant families	7	669**	18**	13*	52**
Between susceptible families	14	559**	77**	39**	56**
Among lines in families	252	82	4	6	8

GENERAL DISCUSSION

In this study, the means and variances of quantitative characters in oats did not return to the recurrent parent by a factor of one-half of the remaining difference between the backcross and recurrent parent means in each succeeding generation. However, the means and variances did, in general, return toward the recurrent parent, although at varying rates for the different characters. Any or all of the following factors may aid in explaining the observed discrepencies:

First, backcross theory is based upon infinite populations, and while the population size in each generation of this study was large compared to a practical backcrossing program, it was small in comparison to infinity. Therefore, it is possible that this "sample" was quite divergent from the infinite population.

Second, diploidy has been assumed in all backcross theory. While some inheritance in oats is diploid in nature, it is unlikely that genes responsible for quantitative characters act as a diploid completely since oats is an allohexaploid species.

Third, theory is based upon such assumptions as additive interaction of loci, complete dominance, equal frequency allelos, equal gene effects between loci, no linkage and no epistasis. Certain of these assumptions are not correct for oats. For example, this study shows that the different quantitative characters are probably controlled by different inter-loci reaction systems.

Fourth, the return to the recurrent parent is usually calculated as percent homozygosity (or heterozygosity) which leads to a reduction by

one-half per backcross generation. Assuming additive, the means return to the recurrent parent by one-half per generation but this is unlikely to be the only genetic system operative. Simple gene models indicate that the variance is reduced in early generations by a factor of less than one-half.

While the number of backcross generations used in this study was too limited to supply a conclusive solution to the use of backcrossing for quantitative characters, encouragement for the plant breeder is found in the results. The means of all characters measured regressed toward the recurrent parent, except yield which showed a persistent increase over the recurrent parent. If the increase for yield should continue through further backcrosses while other characters returned to the recurrent parent phenotype, backcrossing would be useful not only for transferring qualitative characters, but also for producing higher yielding varieties as well. The reduction in yield variance without a reduction in mean yield indicated this to be a possibility.

SUMMARY

In four generations of backcrossing in oats, the mean date of heading, plant height, weight-per-volume and grain yield regressed toward the recurrent parent, but at rates different than expected on the basis of additive gene action alone. Plant height and weight-per-volume returned at a slower rate than expected; date of heading returned faster than expected. Mean yield showed considerable heterosis and no indication of a return toward the recurrent parent. The variances were somewhat erratic, but, in general, they were reduced with additional backcrossing. Height and weight-per-volume variances were reduced very little until the Bc_4 while date of heading and yield variances were higher in the Bc_3 than in the Bc_2 or Bc_4.

Selection for lines with heading dates like the recurrent parent would have been effective in causing all quantitative characters, except weight-per-volume, to return to the recurrent parent phenotype more rapidly than if random crosses had been made. There was no apparent beneficial or detrimental linkage drag associated with the rust resistance gene contributed by the non-recurrent parent.

The means and variances were used to indicate the type of gene action involved in the determination of each character. Date of heading and yield appeared to result from epistatic gene action, whereas weight-per-volume and height resulted from dominance and additive gene action.

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